Food sharing networks in lowland Nicaragua:

An application of the social relations model to count data

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Highlights

- We implement the multilevel Social Relations Model (SRM) for count data as a network response variable.
- We examine gifts of meat exchanged over a yearlong period among 25 households in lowland Nicaragua.
- Food sharing networks largely correspond to kin-based networks of social interaction.
- The results provide support for multiple evolutionary models of food sharing and cooperation.
- We discuss further extensions to the SRM and methodological considerations for related research.

1. Introduction

Compared to other animals, humans have a unique propensity for sharing food, which anthropologists have related to other traits that distinguish humans from other apes (Isaac, 1978; Gurven et al., 2012; Wood and Marlowe, 2013). Food sharing has therefore attracted considerable attention from evolutionary anthropologists (Gurven, 2004; Jaeggi and Gurven 2013). There are multiple hypotheses to explain transfers of food between households, and a common approach is to develop multivariate statistical models that simultaneously test the evidence for these alternative hypotheses (Ziker and Schnegg, 2005; Allen-Arave et al., 2008; Nolin, 2010). Generally, however, these analyses explore only the role of covariates for which there is an unambiguous evolutionary hypothesis. Yet, evolutionary anthropologists are increasingly acknowledging the multifaceted complexities of familial and inter-household relationships and the need for studies that encompass variables other than kinship, differences in production, and reciprocal food exchange (e.g., Gurven and Hill, 2010).

In the current study, we observe transfers of meat over a yearlong period among 25 households in a community of indigenous Mayangna and Miskito horticulturalists in Nicaragua. The data are dyadic and have a "round-robin design" whereby each household interacts with every other household in the community and where we observe the number of transfers given in each direction within each household dyad. We analyze these data using the social relations model (SRM) developed by Kenny and colleagues to separate individual effects from relationship effects in relational or dyadic data (Kenny, 1994). The SRM decomposes the variance in a dyadic outcome into separate giving-, receiving- and relationship- variance components, and allows for correlation in giving and receiving

behaviors as well as for correlation of responses within a dyad. The SRM variance and covariance/correlation parameters are typically estimated by formulating the model as either a structural equation model or a multilevel model. Applied to our data, the SRM estimates the relative importance of households in their role as givers, households in their role as receivers, and unique relationship effects themselves as sources of variation in the number of portions of meat exchanged between households. In addition, the SRM estimates "generalized reciprocity", the degree to which households in general reciprocate transfers, and "dyadic reciprocity", the degree to which transfers are, on average, reciprocated within a dyad. Accessible introductions to the SRM and other models for dyadic data analysis are provided by Kashy and Donnellan (2012), Kenny and Kashy (2010), and Kenny, Kashy and Cook (2006). Van Duijn and Huisman (2011) provide an accessible review and comparison of the SRM to other statistical models for network data, including the Quadratic Assignment Procedure (QAP) and the p_1 and p_2 models. The SRM has been widely applied in social and behavioral research, especially in psychology (Back and Kenny 2010). While evolutionary anthropologists have recently begun to implement multilevel modeling approaches for the analysis of network data (Allen-Arave et al., 2008; Hooper, 2011; MacFarlan et al., 2012; see also Gomes et al., 2009), we are not aware of any prior applications of the SRM to anthropological data from small-scale societies.

In this paper, we make two contributions, one substantive, the other methodological. First, we analyze inter-household meat sharing among indigenous Nicaraguan horticulturalists as a function of multiple predictor variables, including an "association index," which provides a measure of the amount of time that households are spending together and perhaps engaging in mutually beneficial activities. As a related

objective, we assess how the generalized and dyadic reciprocity correlations and the observed variance in the data structure are explained by the covariates. Second, we extend the multilevel modeling formulation of the SRM to accommodate the count data nature of our response variable, and we describe how to fit this model using Bayesian methods as implemented in the free WinBUGS software (Lunn et al., 2000). Standard applications of the SRM are confined to the analysis of continuous responses, and so this extension represents a valuable approach for researchers with dyadic count data, whether on food sharing or other outcomes.

The remainder of the paper is structured as follows. Section 2 discuses theories and predictors of food sharing. Section 3 presents the multilevel modeling formulation of the SRM for count data. Sections 4 and 5 introduce the data and describe the analysis. Sections 6 and 7 present and discuss the results. Section 8 concludes.

2. Theories and predictors of food sharing

2.1. Evolutionary models and predictions

Among humans, but also other animals, food sharing and cooperation more broadly may reflect *kin selection* (the evolutionary strategy of favoring the reproductive success of one's relatives, even at the expense of one's own survival and reproduction). This evolutionary model extends conventional understandings of natural selection to consider the effects of an individual's behavior on the evolutionary fitness (cumulative reproductive success) of their kin (Hamilton, 1964). In other words, even though relinquishing food is costly, the evolutionary benefits of sharing with relatives at the allelic level can be recouped via the reproductive success of genetically similar recipients. Hamilton's Rule

(Hamilton, 1964) indicates that kin selection can occur when $b \times r > c$, where b is the fitness benefit to the receiver, c is the cost to the giver, and r is Wright's coefficient of genetic relatedness (Wright, 1922), or the likelihood of sharing alleles by common descent. Assuming that benefits and costs are held constant, Hamilton's Rule predicts greater altruism and cooperation among close genetic kin, such as the parents, offspring, and full siblings of the giver, than among more distantly related kin or unrelated individuals.

Natural selection can also favor transfers of food between unrelated individuals, particularly if partners enter reciprocal relationships in which they alternately exchange food (Trivers, 1971). Considering the unpredictability with which human foragers successfully acquire fish and game, reciprocal sharing of meat can reduce the day-to-day variability of available meat for such partners (Winterhalder, 1986). A positive correlation between the bidirectional flows within a dyad, generally known as "contingency," provides empirical support for the evolutionary model of *reciprocal altruism* (Gurven, 2004). Owing to the costs of unreciprocated transfers, humans may possess evolved psychological mechanisms that facilitate the detection of cheaters and "free-riders" (Cosmides et al., 2010).

Especially for foods that cannot be stored for long periods of time, such as meat in tropical settings, resources exhibit diminishing marginal valuation (Winterhalder, 1996). Whereas the first portion of a harvest may provide essential nutrients, the value of additional consumption declines as needs are met and physiological constraints prevent individuals from obtaining further nutritional benefits. Such differences in the marginal valuation of portions can promote kin selection and reciprocal altruism, as sated individuals donate remaining portions to kin or reliable partners. Possessors of food might

also relinquish portions to "scroungers" if the cost of defending the resource exceeds the expected marginal value of retaining it. This evolutionary model, known as *tolerated scrounging*, predicts transfers according to differences in need with little expectation of subsequent benefits for the original possessor. Notably, the opportunity to sell portions of meat may attenuate the diminishing value of large resources and reduce the prevalence of tolerated scrounging (Gurven, 2004).

Another evolutionary model, *costly signaling theory*, suggests that possessors of food share widely in order to convey information about their traits, including their generosity or their ability to obtain (and waste) resources (Bliege Bird and Smith, 2005). This information benefits observers, who can subsequently choose the best available mates and allies, which in turn benefits the original signalers. Although the evolutionary logic of costly signaling theory is generally accepted, empirical tests remain challenging because of the need to satisfy multiple conditions of the theory while ruling out alternative hypotheses (Smith and Bliege Bird, 2000).

2.2. Association indices as a predictor of food sharing

Evolutionary anthropologists recognize that food can be "traded" for other fitness-enhancing currencies, such as childcare, political support, reproductive opportunities, help with agricultural labor, or other needed goods and services (Winterhalder, 1996; Gurven, 2004; Patton, 2005; Nolin, 2012). Within cooperative groups, including households as well as broader groupings, the trading of foods for other currencies may promote specialization that promotes group-level efficiency by allocating tasks to the most productive individuals (Gurven, 2004). Such considerations rarely receive formal attention, however, primarily

owing to the challenge of determining the relative costs and benefits of each currency (Winterhalder, 1996).

In addition to scenarios where trades between households are implicit, individuals in small-scale societies cooperate in multiple, beneficial ways. For example, women may forage together, exchanging their insights about the locations of food and boosting overall productivity while also providing emergency assistance and defending each other from external threats (Marlowe, 2010). Within the community, people share tools, build houses together, teach each other skills, jointly care for livestock, and treat others' illnesses. In some cases, such favors entail specific expectations of repayment (i.e., trade), but among close associates, these interactions largely reflect a broader commitment to ongoing relationships in which there is no clear record of debts and credits.

The analysis in this paper hinges on the idea that these multifaceted inter-household relationships provide the social context in which food sharing occurs. Furthermore, we assert that the strength of such relationships is reflected by the amount of time that households spend in each other's company. Time spent together, as measured by an *association index* (Cairns and Schwager, 1987), is not necessarily a causal variable itself. Instead, because cooperation between individuals and households frequently requires direct interaction, the association index serves as a proxy for the multifaceted interdependencies that characterize those relationships.

In prior studies of food sharing in human societies, association indices have received scant consideration as predictor variables. This inattention is surprising given that Wilkinson's (1984) classic study of reciprocal blood regurgitation among vampire bats shows that past association significantly predicts sharing even after controlling for genetic

relatedness. Similar effects are evident among unrelated female hyenas, which show greater tolerance toward frequent associates at feeding sites (Smith et al., 2007). Among non-human primates, affiliative relationships and association predict food sharing among spider monkeys (Pastor-Nieto, 2001) and chimpanzees (de Waal, 1989; Mitani, 2006; Silk et al., 2013; cf. Gilby, 2006; see also Jaeggi et al., 2010) while controlling for kinship.[1]

Among human ecologists, Gurven et al. (2004) provide perhaps the only analysis to consider the relationship between association and food sharing. Their report indicates that, among the Ache of Paraguay, there is a correlation between food sharing in the community and the percentage of time that men spend foraging together in the forest. Because the correlation is limited to food acquired in the forest and foraging expeditions by adult men, however, it is not clear that a similar effect would be apparent when considering other aspects of cooperative relationships and interactions between households.

3. Multilevel social relations model for count data

Consider the number of gifts that Household A gives to Household B. The SRM would decompose this number into four components: (1) the overall mean number of gifts given between households; (2) Household A's giver effect, measuring how the mean number of gifts Household A gives to the other households in the village deviates from the overall mean; (3) Household B's receiver effect, measuring how the mean number of gifts Household B receives from the other households in the village deviates from the overall mean; and (4) Household A and B's unique relationship effect, measuring the number of

[1] de Waal (2000) highlights the need to control for association indices to avoid spurious evidence for reciprocity. See Hawkes et al. (2010) for a similar discussion, but note Gurven and Hill's (2010) observation that the decision to co-reside or spend time together is itself a choice that could be considered a prerequisite to sharing.

gifts that Household A gives to Household B, over and above that suggested by the overall mean and Household A's giver effect and Household B's receiver effect. Conversely, the number of gifts which Household B gives Household A would be decomposed into the overall mean, Household B's giver effect, Household A's receiver effect, and a unique relationship effect from Household B to Household A. The variances of the giver, receiver and relationship effects quantify the relative importance of households as givers, households as receivers, and of the unique relationships themselves as explanations for the observed variance in food giving between households. The correlation between the giver and receiver effects provides a measure of generalized reciprocity: the degree to which food sharing is in general reciprocated (see Gurven, 2004). The correlation between the two unique relationship effects is a measure of dyadic reciprocity: the degree to which excess food sharing is reciprocated within household dyads. That is, the dyadic reciprocity correlation indicates the degree to which a household that gives an especially high number of gifts to another household experiences in return an especially high number of gifts from that household after accounting for households' general giving and receiving tendencies.[2] Thus, the SRM's dyadic reciprocity correlation differs in interpretation as well as calculation from the simple unconditional pairwise correlation one might calculate on the raw data.

Snijders and Kenny (1999) propose multilevel modeling (Goldstein, 2011; Raudenbush and Bryk, 2002; Snijders and Bosker, 2012) as a natural statistical approach for estimating the variance and covariance parameters of the SRM and they demonstrate how to do this using the MLwiN software (Rasbash et al., 2009). Kenny and Livi (2009)

[2] Note that while we expect to find positive dyadic reciprocity, the correlation is allowed to range from -1 to 1 and so is equally able to detect negative dyadic reciprocity.

show how the same multilevel formulation can be implemented in the SAS (SAS Institute Inc., 2012) and SPSS software (IBM Corp, 2012). However, the models they propose are limited to the analysis of continuous response data while our response variable is a count. In contrast, Hoff (2005) shows how the SRM for binary and count responses can be formulated as multilevel logistic and Poisson models, and it is the latter approach that we pursue in this paper. We note that Hoff also proposes an extension to the SRM to allow for limited forms of triadic dependence (transitivity effects), but we do not pursue this extension in the current study. Like Hoff, we employ a Bayesian approach to estimate the parameters of the SRM (see Section 5.4).

Let y_{ij} denote the total number of gifts given by household i $(i = 1, \dots, N)$ to household j $(j = 1, \dots, N)$ over the course of the yearlong study. We model this count outcome as Poisson distributed

$$y_{ij} \sim \text{Poisson}(\mu_{ij}), \tag{1}$$

where μ_{ij} denotes the expected number of gifts given from household i to household j. Thus, the error in this model is the deviation of the observed count from the expected count, $y_{ij} - \mu_{ij}$. We specify the SRM for μ_{ij} as the following log-linear model

$$\log(\mu_{ij}) = \beta_0 + g_i + r_j + d_{ij}, \tag{2}$$

where, for simplicity, we present the "intercept-only" ("null" or "empty") version of the model with no covariates.[3]

[3] Note that equation 2 is specified in terms of μ_{ij} not y_{ij}; we are not attempting to log transform a variable containing zeros. The model assumes there is a non-zero probability of gift giving between each pair of households in the data and so the expected counts for all pairs will exceed zero. If we were instead to believe that there was a truly zero probability of trade between some dyads, as in large networks, then we could in theory test this hypothesis by modeling the counts as following instead a zero-inflated Poisson process, but this is beyond the scope of the current paper.

The intercept parameter, β_0, measures the average logged expected number of gifts given by household i to household j, g_i is a household-level giver random effect which, when added to β_0, measures the average logged expected number of gifts given by household i to other households in the community, r_j is a household-level receiver random effect which, when added to β_0, measures the average logged expected number of gifts received by household j from other households in the community, and d_{ij} is a dyad-level relationship random effect which measures the logged expected number of gifts given by household i to household j above and beyond that predicted by household i's giver effect and household j's receiver effect. Substantive interest lies in estimating the degree to which these different random effects vary and covary across households, as opposed to predicting values for the different random effects for any pair of households. The household-level giver and receiver random effects, g_i and r_i, are assumed bivariate normally distributed with zero means and homogenous 2×2 giver-receiver covariance matrix

$$\begin{pmatrix} g_i \\ r_i \end{pmatrix} \sim \mathrm{N}\left\{ \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_g^2 & \\ \sigma_{gr} & \sigma_r^2 \end{pmatrix} \right\}, \tag{3}$$

where σ_g^2 measures the giver variance, σ_r^2 measures the receiver variance, and σ_{gr} measures the giver-receiver covariance. The corresponding giver-receiver correlation, $\rho_{gr} = \sigma_{gr}/\sqrt{\sigma_g^2 \sigma_r^2}$, measures the degree of generalized reciprocity in the community.

The dyad-level relationship random effects, d_{ij} and d_{ji}, are assumed bivariate normally distributed with zero means and homogenous 2×2 relationship covariance matrix

$$\begin{pmatrix} d_{ij} \\ d_{ji} \end{pmatrix} \sim \mathrm{N}\left\{ \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_d^2 & \\ \sigma_{dd} & \sigma_d^2 \end{pmatrix} \right\}, \tag{4}$$

where σ_d^2 measures the relationship variance; and σ_{dd} measures the covariance. The corresponding correlation, $\rho_{dd} = \sigma_{dd}/\sigma_d^2$, measures the average degree of dyadic reciprocity in the community.

The relative importance of giver, receiver and relationship random effects as sources of variation in gift giving can be summarized by dividing each estimated variance by the total of the three estimated variances. These statistics are referred to in the multilevel modeling literature as variance partition coefficients (VPC, Goldstein et al., 2002).

A complication which arises in the current study is that not all households were present for the full duration of the yearlong study. We account for the variation in the proportion of the year for which both members of each dyad were simultaneously present in the community by entering the natural logarithm of this exposure as an offset in the model (a covariate with coefficient constrained to equal a value of one). This is mathematically equivalent to dividing the expected count in (2) by the exposure. Conceptually this modification allows us to model the expected number of gifts *per year*, rather than the expected number of gifts *per period that each pair of households was present*. The former is more directly interpretable.

The above model can be extended by including household-level covariates to test hypotheses as to why some households generally give or receive more than other households. Note that attributes of the households, such as the amount of hunted game that they harvest, can enter the model twice in order to serve as a predictor of both giving and receiving. Entering dyad-level covariates enable us to test hypotheses as to why some

dyads share more than predicted by their general household-level giving and receiving tendencies. Dyad-level covariates may be symmetric, $x_{ij} = x_{ji}$, or non-symmetric, $x_{ij} \neq x_{ji}$.

4. Study site

The data were collected during a yearlong study in Arang Dak, a community of indigenous Mayangna and Miskito horticulturalists in Nicaragua's Bosawas Biosphere Reserve.[4] At the time of the study (2004-2005), there were approximately 200 residents, distributed among 25 households. Partly owing to the influence of missionaries in the early twentieth century, the Mayangna and Miskito have prescriptively monogamous marriages and a bilateral kinship system that traces descent through both mothers and fathers (Helms, 1971).[5] Households are primarily comprised of married household heads and their offspring, sometimes accompanied by extended kin, including widowed parents of either household head. Although there are no clear postmarital residence rules, it is common for young couples to live with the woman's parents until they have at least one child. Divorces among young couples occur frequently, in which case the woman and offspring typically remain with her parents after the man departs. When building a new house, couples often select locations that are close to the domiciles of other close kin in the community.

Dietary staples include cultivated crops like bananas, plantains, manioc, yams, rice, beans, and maize. Much of the protein in the diet comes from animal-based products. During the study period, hunted meat was the leading source of dietary protein overall

[4] At the time of the study, at least one household head in each household in Arang Dak self-identified as Mayangna. Comparative studies reveal few noteworthy differences in the subsistence strategies of the Mayangna and Miskito (Stocks, 1998).

[5] Bilateral kinship contrasts with a unilineal descent system, in which kin groups are formed and recognized according to descent exclusively from either the father's line (*patrilineal descent*) or the mother's line (*matrilineal descent*).

(Koster, 2007), but whereas hunting is generally limited to a few highly productive households, fishing is a common strategy for virtually all households. The Mayangna and Miskito also keep livestock, including cattle, pigs, and fowl. Cows primarily serve as an exchangeable store of wealth, occasionally sold to itinerant merchants, and they are slaughtered within the community only under unusual circumstances. Pigs and fowl, by contrast, are primarily for consumption. Cows and chickens are also sources of milk and eggs, respectively, but these animal by-products are secondary foods in this setting.

Other anthropologists have commented on the food sharing norms of the Miskito. Nietschmann (1973) notes that meat is shared more widely than cultivated crops, which is a common cross-cultural pattern (Gurven, 2004). Both Nietschmann (1973) and Helms (1971) indicate that close kin are the primary recipients of shared food, with special emphasis on mothers, followed by married offspring, siblings, and aunts. Reflecting the importance of the church in community life, residents also donate food to the communities' pastors (Helms, 1971), who are typically local men with little formal religious training outside of periodic participation in territory-wide workshops and gatherings. Helms (1971) also credits the Christian influence and an ethic of generosity for the charitable support of the poorest households in the community. More generally, Nietschmann (1973) describes a redistributive system in which the most productive hunters and fishermen give away considerably more than they receive over intermediate periods of time.

5. Methods and analysis

5.1. Data collection

Throughout the study period, local research assistants worked with female household heads every morning to document the acquisition and consumption of animal-based foods, including meat, eggs, and milk. When such foods had been consumed in the previous 24 hours, the assistants recorded whether it was produced by a member of that household or whether it was a purchase or a gift and the identity of the provider. Each time a resource was consumed, it was documented as a "portion" (analogous to the "consumption events" of Kaplan and Hill, 1985). For purchases, Nicaraguan currency is often the unit of exchanges, but purchases can also be made via bartered goods or services. In this paper, we focus only on gifted foods, which entail no immediate and specific expectations of exchange or reciprocity.

The aforementioned animal products vary in the extent to which portions are gifted, sold, or retained by the possessing household (Fig. 1). For example, more than half of the consumed portions of hunted game were received as gifts from other households. By contrast, only 21% of the portions of fish were received as gifts. Such differences probably reflect variation in the "package size" of the respective resources, as the marginal valuation promotes the apportionment and distribution of large items (Tucker, 2004).[6] Also, unlike hunting, fishing returns are seasonally predictable, which depresses the benefits of sharing (or scrounging) because households tend to have similar amounts of harvested fish at any particular time (see Winterhalder, 1996).

[6] Relative to hunted game, proportionally fewer portions of pork are retained by the household that slaughtered the pig. One important difference between these resources is that, whereas only adult pigs are routinely slaughtered, there is a wide variety of harvested game species that vary in size (Koster, 2008*a*). It is reasonably clear that smaller game animals are more likely to be consumed entirely by the acquiring household.

Other methods result in complementary data. For approximately one week per month, the lead author used the "spot check" observational method to document the behavior of residents (Koster et al., 2013). This method entails unannounced and randomly scheduled observations of households, during which the activities and locations of all residents are recorded (Borgerhoff Mulder and Caro, 1985). In this study, observations occurred on 82 days between 5:30 AM and 6:00 PM, and households were sampled without replacement such that all households were sampled exactly once per day (see Koster et al., 2013). During the observations, the interactions of household members with any other person in the community were recorded. For example, if the male household head from Household A was fishing with an adolescent boy from Household B, this interaction was documented. These observed interactions provide the basis for an inter-household association index (see below).

Periodic censuses of the community throughout the study period provide data on livestock ownership. For the duration of the project, local research assistants documented the harvest of fish and game by all members of the community (Koster, 2008*b*). Informant rankings on an ordinal scale were used to calculate a weighted average of each household's wealth, which is correlated with household ownership of material possessions (Koster, 2011*a*). Genealogical interviews were used to calculate the purported genetic relatedness of all residents. A GPS unit was used to map the locations of households, thus facilitating the calculation of inter-household distance, which ranges from 17 to 357 meters (mean = 122 meters).

5.2 Calculation of the association index

We used the spot check observational data to create an inter-household "association index" (Cairns and Schwager, 1987). We summed all of the times in which a member of Household A was observed interacting with Household B, which produces a valued symmetric matrix. Largely because of differences in household size, we normalized the matrix using an iterative process in UCINET (Borgatti et al., 2002). This normalization ensures that the marginal sums of all rows and columns are approximately equal to one, thereby giving all nodes "equal weight" (Hanneman and Riddle, 2005; see Alvard, 2003 for a similar application of this normalization procedure).

5.3. Modeling strategy, covariates, and predictions

Our foremost interest lies in the effect of the association index, but to avoid spurious interpretations, we include a broader suite of covariates (i.e., "fixed effects") that are likewise expected to account for variation in meat sharing (see Table 1 for descriptions and summary statistics). These covariates include variables that are routinely included in studies of food sharing, such as kinship and inter-household distance. Other predictors reflect attributes and relationships that have been noted in the ethnographic literature on food sharing in lowland Nicaragua.

Some covariates are household-level attributes, referring to characteristics of either the giving household or the receiving household. Other covariates are dyadic in the sense that they refer to the relationships between household pairs, such as inter-household kin relations, distance, or the association index.[7]

[7] In studies of food sharing, dyadic variables tend to be symmetric, such that the value of the variable from household A to B equals the value from household B to A. Our dyadic variables for kinship are symmetric, for example. As noted previously, however, asymmetric variables could also be included. For example,

Like Nolin (2010), we include distance primarily as a control variable, with the expectation that transfers will decrease with increasing distance between households. Because these distances exhibit positive skew, this variable was log-transformed prior to analysis.

Transfers are expected to be higher between households that are more closely related. We characterize the kin-based relationship between households using the coefficient of relatedness, r, associated with the closest kin tie between each household dyad. Given the ethnographic commentary on the importance of mother-offspring ties, we distinguish such relationships from sibling and father relationships even though all three relationships are characterized by the same coefficient of relatedness.[8] Specifically, we enter the coefficient of relatedness as a series of four dummy variables: (1) mother-offspring ties, $r = 0.5$; (2) father-offspring and full sibling ties, $r = 0.5$; (3) other close kin ties where $r \in [0.25, 0.5)$; (4) weaker ties where $r \in [0.1, 0.25)$. The omitted reference category relates to unrelated household dyads or those with the weakest ties, $r \in [0, 0.1)$.

Whether motivated by tolerated scrounging or costly signaling, we anticipate redistributive transfers from households with relatively more meat to those with less. Similarly, the aforementioned ethic of generosity among the Mayangna and Miskito would stimulate transfers from wealthier households to poorer households. Several of our covariates speak to these imbalances of resources, including harvest of fish and game, ownership of pigs, and the wealth rankings. In all cases, we predict giving to increase with increased resources and for receiving to decrease with increased resources.

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primatologists could employ a variable to distinguish the "dominant to subordinate" relationship from the "subordinate to dominant" relationship within a dyad of the same two individuals (e.g., Range and Noë, 2002).

[8] Of the 36 dyads in the "siblings and fathers" category, only one is characterized by a father-offspring tie. The other 35 dyads have full sibling ties.

Based on ethnographic reports of donations to pastors (Helms, 1971), we include a binary variable to denote the recipient households in which the community's two pastors reside.

There are no clear evolutionary predictions for the estimate of generalized reciprocity (Gurven, 2004), but following the logic of marginal models (Winterhalder, 1996), we predict a negative estimate as transfers flow from the "haves" to the "have-nots." Under the assumption that household-level production of meat varies more than households' nutritional needs, we also anticipate a redistributive system in which the estimated giver-level variance exceeds the receiver-level variance. Similar differences in variance seem to characterize other networks in small-scale societies (Kasper et al., manuscript).

In terms of dyadic reciprocity, we predict that the estimated correlation will be positive, which would support reciprocal altruism.

The random effects in these models are assumed to be normally distributed, but there was a noteworthy outlier in the relationship-level random effects. We therefore include a dummy variable to represent this outlier as a fixed effect (Langford and Lewis, 2002). We discuss this outlier when we interpret the results.

5.4. Estimation

We fit our count data SRM using Markov chain Monte Carlo (MCMC) methods as implemented in the WinBUGS statistical software package (see Supplementary File 2 for a full description of how the models were fitted in WinBUGS; cf, Gill and Swartz, 2001, and Lüdtke et al., 2013 who both fit the standard SRM for continuous response data using

WinBUGS). We call WinBUGS from within Stata using the user written winbugs command (Thompson et al., 2006). We specify "diffuse" (i.e. "flat" or "uninformative") prior distributions for all parameters. We run the models in WinBUGS for a burn-in of 50,000 iterations to allow the chains to converge to their stationary distributions. We judge convergence by informal visual assessments of the parameter chains and through examining standard MCMC convergence diagnostics. The plots (not shown here) suggest the chains achieved stationarity well before 50,000 iterations. We then sampled 100,000 iterations. When we present our results, we report the means, standard deviations and 2.5th and 97.5th quantiles (95% credible intervals) of the 100,000 monitoring iterations. These quantities are analogous to the parameter estimates, standard errors and lower and upper bounds of the 95% confidence intervals obtained in a frequentist analysis. We compare the fit of models via the deviance information criterion (DIC; Spiegelhalter et al., 2002): models with smaller DIC values are preferred to those with larger values, with differences of five or more considered substantial (Lunn et al., 2012).

6. Results

We present two models. Model 1 is the intercept-only model presented in Section 3 and is used to quantify the relative importance of givers, receivers and unique relationships as sources of variation in household giving. Model 2 includes the association index and adjusts for the other household- and dyad-level covariates described in Section 5. Table 2 presents the results.

6.1 Model 1 – The intercept-only model

The intercept, β_0, is estimated to be 0.68. The population-averaged number of gifts given per year, $\mathrm{E}(\mu_{ij}) = \exp\{\beta_0 + \frac{1}{2}(\sigma_g^2 + \sigma_r^2 + \sigma_d^2)\}$, is therefore estimated to be $\exp\{0.68 + \frac{1}{2}(0.66 + 0.26 + 1.25)\} = 5.84$.[9] This estimate slightly exceeds the average annualized observed rate of 5.46 gifts per year, reflecting the presence of some excess zeros in the data.

The giver VPC, $\sigma_g^2/(\sigma_g^2 + \sigma_r^2 + \sigma_d^2)$, is estimated as $0.66/(0.66 + 0.26 + 1.25) = 0.30$ and so 30% of the variation in food transfers lies between households in their roles as givers. The receiver and relationship variances are estimated to account for 12% and 58% of the variation, respectively. Thus households vary more in how much they give than in how much they receive. However, it is the unique relationships between households which are the main source of variation in food transfers in these data. The statistical significance of each variance component is shown by a large increase in the DIC statistic when we omit the corresponding set of random effects from the model.

Generalized reciprocity, ρ_{gr}, is estimated to be -0.48 and so households who tend to give more gifts than average tend to receive less gifts than average and vice versa. This suggests a process of redistribution whereby some households are net givers of food, while others are net receivers.

Dyadic reciprocity, ρ_{dd}, is estimated to be 0.95 and so when one household gives an especially high number of gifts to another household, that behavior is nearly always reciprocated.

[9] To calculate this prediction, we integrate out the random effects by making use of the fact that if a random variable is log normally distributed with mean μ and variance σ^2, then its expected value is given by $\exp(\mu + \frac{1}{2}\sigma^2)$.

6.2 Model 2 – Including household- and relationship-level covariates

Model 2 shows a reduction in the DIC statistic of $2245 - 2198 = 47$ points, confirming that collectively the covariates improve the fit of the model.

Households who harvest more game ($\beta_1 = 0.45$) and own more pigs ($\beta_3 = 0.12$) are predicted to give significantly more gifts than households who harvest less game and own less pigs. However, there is no significant relationship between fish harvest ($\beta_2 = 0.27$) or overall household wealth ($\beta_4 = 0.01$) and giving, having adjusted for the other factors in the model.

There is no significant association between the amount of game ($\beta_5 = -0.10$) or fish ($\beta_6 = -0.77$) that households harvest or the number of pigs they own ($\beta_7 = -0.06$) and the number of gifts they tended to receive from other households. However, households whose overall wealth was higher were predicted to receive significantly fewer gifts ($\beta_8 = -0.05$). The two pastors' households were predicted to receive significantly more gifts ($\beta_9 = 0.79$) than the other households.

There is a significant positive monotonic relationship between genetic relatedness and giving. Figure 2 plots the predicted number of gifts by genetic relatedness to give a better sense of this relationship. Transfers are biased toward close kin, especially between households that have mother-offspring ties ($\beta_{10} = 1.47$). Furthermore, the model predicts greater transfers between households with full sibling or father-offspring ties ($\beta_{11} = 0.94$) than households that have moderately weaker genetic ties ($\beta_{12} = 0.27$), which is consistent with kin selection. The effects of kinship are quickly attenuated, however, as households with cousin ties ($r = 0.125$) exhibit propensities for sharing ($\beta_{13} = 0.01$) that are undifferentiated from the reference category, dyads without noteworthy kin ties.

Households located farther apart are predicted to give less ($\beta_{14} = -0.63$) than nearby households. Distance is entered as a log-transformed variable and so its coefficient has a partial elasticity interpretation: a 10% increase in the distance between two households is associated with a 6.3% decrease in the expected number of gifts exchanged between the two households. Regarding the association index, households who associated more frequently with one another were predicted to give more ($\beta_{15} = 4.02$), even after adjusting for their higher genetic relatedness and closer proximity. The positive estimate relating to the outlying dyad ($\beta_{16} = 2.47$), shows that the number of gifts given between Household 1 and Household 25 was significantly higher than that predicted by the model. This outlying dyad was comprised of two households that lacked a close kinship tie and that lived relatively far from each other, but each exhibited a close relationship with the household that produced more hunted game than any other household in the community, and there may have occasionally been expectations that transfers to one member of the dyad would also entail secondary transfers to the other.

The giver, receiver and relationship variances, σ_g^2, σ_r^2 and σ_e^2, are now estimated to be 0.30, 0.18 and 0.29, respectively. Comparing these results to Model 1, shows that adjusting for the household and relationship characteristics explain away $(0.66 - 0.30)/0.66 = 0.55$ or 55% of the variation in giving behavior between households, 31% of the variation in receiver behavior and 77% of the variation in relationship behavior.

Generalized reciprocity, ρ_{gr}, is now estimated to be 0.08, substantially lower in absolute value than the estimate of -0.48 reported in Model 1, and the correlation is no longer significantly different from zero. Thus, the pattern of negative generalized

reciprocity seen in the empty model is explained by the inclusion of the giver and receiver characteristics; the covariates explain why households are net givers or receivers of food.

Dyadic reciprocity, ρ_{dd}, is now estimated to be 0.77, lower than the estimate of 0.95 reported in Model 1. Nevertheless, even after accounting for the genetic relatedness of the households in each dyad as well as their physical distance apart and association index, we continue to see a very strong relationship whereby when one household gives an especially high number of gifts to another household, that behavior is very often reciprocated.

7. Discussion

7.1 Substantive findings

Households that spend greater amounts of time together also exchange meat more frequently, as reflected by the strong statistical support for the association index as a predictor of meat sharing. This result underscores the extent to which food sharing is embedded in broader social relationships between households. Ethnographic observations suggest that food sharing is particularly common among households that regularly engage in mutually advantageous activities, such as cooperative childcare and collaborative agricultural labor. As noted previously, it is possible that sharing meat acts as a form of trade for other currencies. Alternatively, sharing meat could serve partly as a signal of commitment to the long-term maintenance of the relationship (see Nolin, 2010). Although the underlying mechanisms remain unclear, the significant effect of the association index highlights the need for future research to situate food sharing within the context of broader inter-household relationships.

Despite exhibiting a strong positive effect on sharing, the association index does not greatly increase the predictive accuracy of the full model, as the DIC improves by only 1 unit when compared to a model that lacks the association index (Supplementary File 1, Table S1). This seemingly contradictory result reflects the strong correlation between the association index and the categorical variables for kinship ties between houses (Supplementary File 1, Figure S1). In other words, household dyads that spend considerable time together typically have close kinship ties, particularly mother-offspring ties or sibling ties. As a result of the collinearity, the effects of the variables for kin ties are mitigated when the association index is included in the statistical model. Rather than characterizing the association index as redundant with kinship as a predictor of food sharing, these models are a reminder that kinship frequently structures the patterns of social organization and interaction in small-scale societies, not only in terms of food sharing but also in the formation of cooperative social groups (Hames, 1987; Alvard, 2009). The main insight from the analysis in this paper is that food sharing networks in Arang Dak largely coincide with the kin-based networks of social interaction and grouping. Whereas other studies have shown that households with close kinship ties exhibit greater reciprocity of food sharing than distantly related household dyads (Allen-Arave et al., 2008; see also Nolin, 2010), this study demonstrates that closely related households spend more time together and therefore have more opportunities to resolve imbalances of food transfers via trade, not just via reciprocated food.

In addition to the association index, other covariates exhibit noteworthy effects that support multiple evolutionary models of food sharing. As with the research of Silk et al. (2013) on chimpanzees, we conclude that people share food for many reasons. For

instance, the categorical variables for kinship ties are consistent with kin selection. The results also provide evidence in support of a redistributive model of food sharing, as households that regularly harvest game and own more pigs give greater amounts of meat to other households. Although these redistributive flows from houses with large quantities of meat could reflect trades for unidentified currencies, our ethnographic perspective is that meat is typically given without clear expectations of repayment, and these patterns might better be characterized as investments in long-term mutualistic relationships, or perhaps as tolerated scrounging or costly signaling (cf. Koster, 2011*b*). In contrast to hunted game and ownership of pigs, variation in harvests of fish does not predict meat sharing, which we partly attribute to the relatively small proportion of fish that are transferred as gifts (as in Figure 1). The wealth ranking of giving households is also an uninformative predictor, apparently because wealth does not reliably correlate with supplies of transferable meat. On the other hand, the wealth ranking of receiving households exhibits a negative effect, as poorer households receive significantly more gifts than their wealthier counterparts. This result might reflect need-based transfers to households with few options for purchasing meat. As in several other studies (Gurven et al., 2000; Ziker and Schnegg, 2005; Hames and McCabe, 2007; Allen-Arave et al., 2008; Nolin, 2010), food sharing increases with increasing proximity between households, which is noteworthy given that the model controls for other relationship-level covariates that are correlated with distance, including kinship and the association index (cf. Patton, 2005; Hames and McCabe, 2007). Although distance lacks a clear evolutionary interpretation, there are numerous beneficial ways in which neighbors can cooperate, such as

collaborative vigilance against thieves, which could plausibly promote gifts of meat that help to maintain amicable relationships with neighbors.

Evolutionary anthropologists have generally examined generalized reciprocity by testing the correlation between the corresponding marginal sums from a sociomatrix (Gurven et al., 2002). The Social Relations Model, by contrast, derives the generalized reciprocity correlation from the giver and random effects, which advantageously offers the opportunity to determine how the correlation changes upon the inclusion of covariates. In the intercept-only model, the generalized reciprocity correlation is negative, as households that give frequently receive comparatively less in return. This effect becomes negligible with the inclusion of the covariates, and a related analysis by Koster (2011*b*) leads us to infer that the weakening of the correlation in the full model largely reflects the inclusion of the variable for the giving households' harvests of hunted game.

In the Social Relations Model, reciprocity in unique relationships is assessed via the dyadic reciprocity correlation, which circumvents the undesirable practice of treating transfers between households as both an outcome and predictor variable in the same statistical model, as in several previous studies of food sharing (for a discussion, see Gurven et al., 2000). In the models presented here, the dyadic reciprocity correlation reveals considerable reciprocal meat sharing between households, even after adjusting for other covariates. These results therefore provide clear evidence for the contingent transfers that characterize reciprocal altruism (Gurven, 2004). When interpreting this correlation, it is important to remember that the model is simultaneously estimating the random effects for households' respective giving and receiving tendencies. The correlation

therefore represents the extent to which dyads exchange gifts beyond what would be expected from these tendencies.[10]

Although evolutionary anthropologists typically regard behavior as an adaptive response to local environmental conditions (Winterhalder and Smith, 2000), there is increasing recognition that behavior is influenced by cultural norms that may deviate from the optimal evolutionary strategy (e.g., Tucker, 2012). In this study, the residents of Arang Dak exhibit sharing behavior that parallels behavior observed by other anthropologists who have worked with the Miskito (Helms 1971; Nietschmann 1973). In particular, the practices of giving considerable food to mothers, pastors, and poorer households are apparently consistent social norms that persist over decades in this society. Furthermore, the coastal Miskito studied by Nietschmann (1973) exhibit maritime subsistence strategies that differ substantially from those in Arang Dak, including the seasonal exploitation of sea turtles versus an orientation toward terrestrial hunting, which may pose challenges for the view of food sharing strategies as an adaptive pattern that closely corresponds to local socio-ecological conditions. We hesitate to portray these norms as maladaptive, particularly given evidence that charitable giving can adaptively enhance reputations (Barclay, 2011). This study nevertheless highlights the need for evolutionary anthropologists to devote increased attention to the cultural transmission of food sharing norms.

7.2 Methodological extensions

[10] If we modify the intercept-only model to exclude the random effects (varying intercepts) for giving and receiving households, then the dyadic reciprocity correlation is reduced from 0.95 to 0.34.

In this paper we have applied an adaptation of the SRM for count data. As in standard applications of the SRM to continuous data, we have modeled the giver, receiver and relationship variances as well as the generalized and dyadic reciprocity correlations as homogenous parameters. One interesting extension would be to include random coefficients (varying slopes) in order to model these parameters as functions of the covariates. We could, for example, then model whether dyadic reciprocity increases with the genetic relatedness of household dyads (Allen-Arave, et al., 2008).

A second extension would be to model not only the number of portions gifted between households, but, simultaneously, the number of portions which are sold from one household to another as well as the number of portions which are simply retained. One approach would be to treat these data as multinomial grouped data where the number of "trials" is the total number of portions in each household, while the "number of successes" in each "outcome category" are given by the counts of the number of portions given, sold and retained. We can then introduce covariates into this model to test hypotheses as to the factors which predict household-level decision making.

A third possible extension would be to extend the model to a longitudinal dyadic data analysis and then analyze the month-by-month counts rather than the annual total counts considered here. One could then look at the stability of parameter effects over time and explore whether there are seasonal trends in household giving and receiving tendencies (see Ward and Hoff, 2007; Ward et al., 2013). A longitudinal framework would potentially also allow one to explore dynamic tit-for-tat patterns of reciprocity in addition to contemporaneous reciprocity addressed here. Alternatively, social network statistical

models could be fitted to these data; in particular Snijder's SOAM model (Snijders, 1996) could be used to model the month-by-month evolution of the food sharing network.

8. Conclusion

In recent decades, evolutionary anthropologists have shown that the structures of food sharing networks in small-scale societies often conform to predictions derived from evolutionary hypotheses, such as kin selection and reciprocal altruism. The analysis in this paper provides additional support for those evolutionary perspectives while also elucidating thematic extensions and statistical alternatives that could enhance future research on food sharing. Evolutionary anthropologists are admittedly reductionist, typically employing heuristic models that parallel those used by economists and focusing primarily on covariates with straightforward evolutionary interpretations (Winterhalder and Smith, 2000). Our analysis, however, reveals that food sharing networks are embedded in broader inter-household relationships that encompass a broad array of social interactions and culturally-mediated roles. Much like Granovetter (1985) encouraged economists to consider the social context of economic transactions, we therefore highlight the need for evolutionary anthropologists to devote greater attention to the emergence and maintenance of cultural norms that influence food sharing, such as distinctions between genetic and cultural kinship and the introduction of norms by missionaries and other external agents.

Statistically, the SRM represents a promising alternative to matrix permutation methods and multilevel modeling approaches that do not fully accommodate the structure

of network data.[11] We presented a version of the SRM that is appropriate for count data, but we note that the advantages of the SRM would apply equally to continuous or dichotomous outcomes. We have also discussed possible extensions of the SRM, which could likewise be implemented for a variety of outcome types, that could further enrich the analysis of the highly detailed datasets that characterize ethnographic research by anthropologists in small-scale societies.

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Barclay, P., 2011. The evolution of charitable behaviour and the power of reputation. In Roberts, C. (Ed.), Applied evolutionary psychology. Oxford University Press, pp. 149-72.

[11] In general, we discourage evolutionary anthropologists from using matrix permutation methods like the Quadratic Assignment Procedure because, although the permutations account for the statistical non-independence of network data, the coefficients and measures of fit in these models are estimated as though the data are statistically independent. When using QAP methods that are estimated via OLS regression methods, there is also a tendency to deemphasize or ignore assumptions about homoscedasticity and the normality of residuals. For these reasons, the analysis in this paper supersedes the earlier MRQAP analysis that the lead author presented on a related subset of these data (Koster, 2011*b*).

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FIGURE LEGENDS

Fig. 1. For each resource type, the total number of portions that were given to other households, sold to other households, or consumed within the household that produced the resource. The analysis in this paper is based only on the sum of gifted portions (regardless of resource type) exchanged between households, not sold or household portions.

Fig. 2. Predicted number of gifts per year by household dyad closest relatedness tie: (1) mother-offspring ties ($r = 0.5$); (2) father-offspring and sibling ties ($r = 0.5$); (3) other ties where $r \in [0.25, 0.5)$; (4) other ties where $r \in [0.125, 0.25)$; (5) other ties where $r \in [0, 0.125)$. These predictions are calculated holding all other covariates at their mean values, with the exception of the outlier dummy variable and the pastor effect, which are set to zero. We integrate out the giver, receiver and relationship random effects.

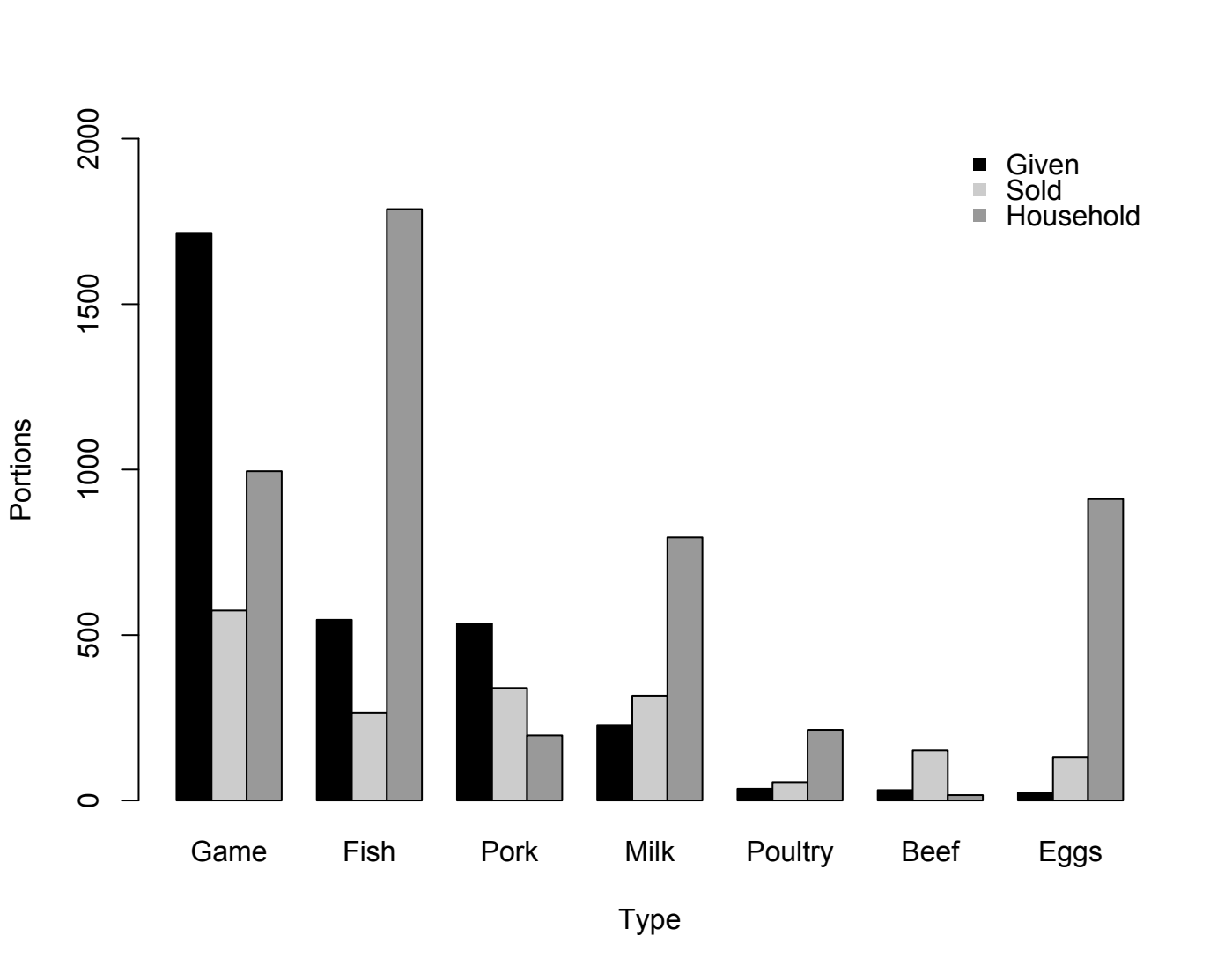
Given
Sold
Household
Portions
0
500
1000
1500
2000
Game
Fish
Pork
Milk
Poultry
Beef
Eggs
Type

Table 1. Variable names, descriptions and summary statistics

Variable	*Description*	*N*	*Mean*	*Std. Dev.*	*Min*	*Max*
Household-level						
Game	Kg meat harvested per day	25	0.79	1.43	0.01	6.09
Fish	Kg fish harvested per day	25	0.25	0.19	0.03	0.74
Pigs	Average # of pigs owned during study period	25	3.58	2.62	0.00	9.50
Wealth	Household wealth index	25	15.27	6.20	7.27	27.4
Pastors	Dummy variable to denote a pastor in the receiving household	25	0.08		0.00	1.00
Relationship-level						
Relatedness1	Dummy variable to denote closest tie is a mother-offspring tie ($r = 0.5$)	600	0.06		0.00	1.00
Relatedness2	Dummy variable to denote closest tie is a father-offspring or full sibling tie ($r = 0.5$)	600	0.12		0.00	1.00
Relatedness3	Dummy variable to denote closest tie has $r \in [0.25, 0.5)$	600	0.21		0.00	1.00
Relatedness4	Dummy variable to denote closest tie has $r \in [0.1, 0.25)$	600	0.26		0.00	1.00
Distance	Distance (km) between the two households, log transformed	600	0.12	0.06	0.02	0.36
Association	Index of frequency with which the two households interact	600	0.04	0.08	0.00	0.55

Table 2
Results for Models 1 and 2.

Parameter		Model 1		Model 2	
		Mean	Std. Dev.	Mean	Std. Dev.
β_0	Intercept	0.68	0.16	-0.92	0.63
β_1	Giver – Game	–	–	**0.45**	**0.08**
β_2	Giver – Fish	–	–	0.27	0.77
β_3	Giver – Pigs	–	–	**0.12**	**0.05**
β_4	Giver – Wealth	–	–	0.01	0.02
β_5	Receiver – Game	–	–	-0.10	0.07
β_6	Receiver – Fish	–	–	-0.77	0.58
β_7	Receiver – Pigs	–	–	-0.06	0.04
β_8	Receiver – Wealth	–	–	**-0.05**	**0.02**
β_9	Receiver – Pastors	–	–	**0.79**	**0.37**
β_{10}	Relationship – Relatedness1	–	–	**1.47**	**0.26**
β_{11}	Relationship – Relatedness2	–	–	**0.94**	**0.17**
β_{12}	Relationship – Relatedness3	–	–	**0.27**	**0.14**
β_{13}	Relationship – Relatedness4	–	–	0.01	0.14
β_{14}	Relationship – Distance (log transformed)	–	–	**-0.63**	**0.08**
β_{15}	Relationship – Association index	–	–	**4.02**	**0.65**
β_{16}	Relationship – Giver 1 & Receiver 25	–	–	**2.47**	**0.62**
σ_g^2	Giver variance	**0.66**	**0.22**	**0.30**	**0.11**
σ_r^2	Receiver variance	**0.26**	**0.09**	**0.18**	**0.07**
σ_d^2	Relationship variance	**1.25**	**0.13**	**0.29**	**0.04**
ρ_{gr}	Generalized reciprocity correlation	**-0.48**	**0.19**	0.08	0.24
ρ_{dd}	Dyadic reciprocity correlation	**0.95**	**0.03**	**0.77**	**0.10**
	Giver VPC (relative variance)	**0.30**	**0.07**	**0.39**	**0.08**
	Receiver VPC (relative variance)	**0.12**	**0.04**	**0.23**	**0.07**
	Relationship VPC (relative variance)	**0.58**	**0.07**	**0.38**	**0.07**
DIC	Deviance Information Criterion	2245		2198	

Note: All models are run for a burn-in of 50,000 iterations and a monitoring chain of 100,000 iterations. Diffuse prior distributions are specified for all parameters. Parameters in bold represent effects whose 95% credible intervals do not include zero (or, in the case of the three variance parameters, whose DIC statistics increase by five or more points) and are therefore viewed as statistically significantly different from zero.

Supplementary Table S1
Results for Model 2a, which parallels Model 2 except for the omission of the association index as a covariate.

Parameter		Model 2a Mean	Model 2a Std. Dev.
β_0	Intercept	-1.03	0.68
β_1	Giver – Game	**0.47**	**0.08**
β_2	Giver – Fish	0.16	0.82
β_3	Giver – Pigs	**0.13**	**0.06**
β_4	Giver – Wealth	0.00	0.02
β_5	Receiver – Game	-0.08	0.07
β_6	Receiver – Fish	-0.74	0.65
β_7	Receiver – Pigs	-0.05	0.05
β_8	Receiver – Wealth	**-0.05**	**0.02**
β_9	Receiver – Pastors	**0.73**	**0.37**
β_{10}	Relationship – Relatedness1	**2.55**	**0.21**
β_{11}	Relationship – Relatedness2	**1.30**	**0.17**
β_{12}	Relationship – Relatedness3	**0.40**	**0.15**
β_{13}	Relationship – Relatedness4	0.08	0.15
β_{14}	Relationship – Distance (log transformed)	**-0.69**	**0.09**
β_{15}	Relationship – Association index	–	–
β_{16}	Relationship – Giver 1 & Receiver 25	**2.73**	**0.70**
σ_g^2	Giver variance	**0.35**	**0.13**
σ_r^2	Receiver variance	**0.19**	**0.08**
σ_d^2	Relationship variance	**0.38**	**0.05**
ρ_{gr}	Generalized reciprocity correlation	0.23	0.25
ρ_{dd}	Dyadic reciprocity correlation	**0.81**	**0.08**
	Giver VPC (relative variance)	**0.38**	**0.08**
	Receiver VPC (relative variance)	**0.21**	**0.07**
	Relationship VPC (relative variance)	**0.41**	**0.07**
DIC	Deviance Information Criterion	2199	

Note: All models are run for a burn-in of 50,000 iterations and a monitoring chain of 100,000 iterations. Diffuse prior distributions are specified for all parameters. Parameters in bold represent effects whose 95% credible intervals do not include zero and are therefore viewed as statistically significantly different from zero.

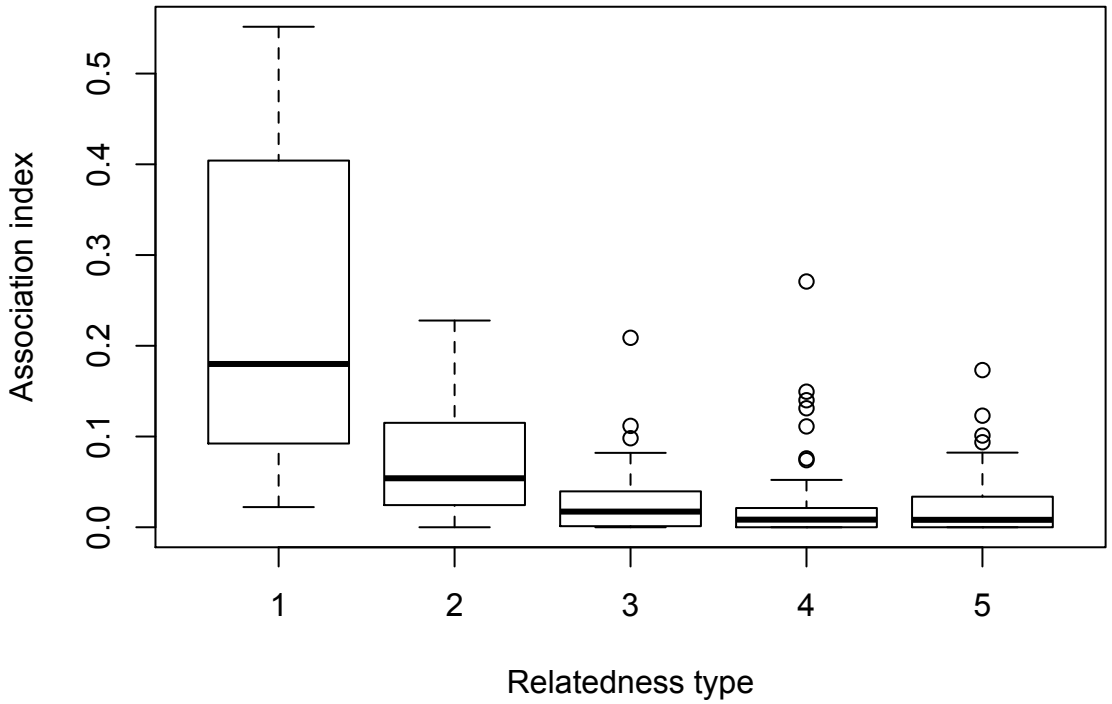

Fig S1. For 300 household dyads, boxplot of association index by the household dyad's closest relatedness tie: (1) mother-offspring ties ($r = 0.5$); (2) father-offspring and sibling ties ($r = 0.5$); (3) other ties where $r \in [0.25, 0.5)$; (4) other ties where $r \in [0.125, 0.25)$; (5) other ties where $r \in [0, 0.125)$

Supplementary file 2 – Fitting the Multilevel SRM for count data in WinBUGS

To fit the SRM in WinBUGS, we must first write the necessary WinBUGS model specification, data and initial values files. We then write a WinBUGS script file that loads these three files, specifies the burn-in and monitoring periods for the MCMC chain, and specifies the name of the output files where the MCMC chains will be automatically stored. [i] The WinBUGS language used in these text files is easy to read and is similar to the popular R language used in the R general-statistical package. Below, we describe the files for Model 2. We then show how to run these files in WinBUGS to replicate the presented results.[ii] The WinBUGS Manual (Spiegelhalter et al., 2003) and the text books by Lunn et al. (2012) and Ntzoufras (2009) provide accessible introductions to the WinBUGS software.

Model specification file

The "model specification file", named `model2.txt`, specifies the model using a series of statements written within a single overall model statement:

```
model{

  # Dyadic response distributions
  for(d in 1:300) {

    # Observed gifts from A to B modeled as Poisson distributed
    giftsAB[d] ~ dpois(muAB[d])

    # Observed gifts from B to A modeled as Poisson distributed
    giftsBA[d] ~ dpois(muBA[d])

    # Linear predictor for log of expected gifts from A to B
    log(muAB[d]) <- offset[d]
                  + beta[1]
                  + beta[2]*hgame[hidA[d]]
                  + beta[3]*hfish[hidA[d]]
                  + beta[4]*hpigs[hidA[d]]
                  + beta[5]*hwealth[hidA[d]]
                  + beta[6]*hgame[hidB[d]]
                  + beta[7]*hfish[hidB[d]]
                  + beta[8]*hpigs[hidB[d]]
                  + beta[9]*hwealth[hidB[d]]
                  + beta[10]*hpastor[hidB[d]]
                  + beta[11]*drel1[d]
                  + beta[12]*drel2[d]
                  + beta[13]*drel3[d]
                  + beta[14]*drel4[d]
                  + beta[15]*dlndist[d]
```

```
                + beta[16]*dass[d]
                + beta[17]*d0125[d]
                + gr[hidA[d],1] + gr[hidB[d],2] + dd[d,1]

  # Linear predictor for log of expected gifts from B to A
  log(muBA[d]) <- offset[d]
                + beta[1]
                + beta[2]*hgame[hidB[d]]
                + beta[3]*hfish[hidB[d]]
                + beta[4]*hpigs[hidB[d]]
                + beta[5]*hwealth[hidB[d]]
                + beta[6]*hgame[hidA[d]]
                + beta[7]*hfish[hidA[d]]
                + beta[8]*hpigs[hidA[d]]
                + beta[9]*hwealth[hidA[d]]
                + beta[10]*hpastor[hidA[d]]
                + beta[11]*drel1[d]
                + beta[12]*drel2[d]
                + beta[13]*drel3[d]
                + beta[14]*drel4[d]
                + beta[15]*dlndist[d]
                + beta[16]*dass[d]
                + beta[17]*d0125[d]
                 + gr[hidB[d],1] + gr[hidA[d],2] + dd[d,2]

}

# Giver and receiver bivariate normal random effects
for (h in 1:25) {
  gr[h,1:2] ~ dmnorm(zero[1:2],TAU_gr[1:2,1:2])
}
zero[1] <- 0
zero[2] <- 0

# Relationship bivariate normal random effects
for(d in 1:300) {
  dd[d,1:2] ~ dmnorm(zero[1:2],TAU_dd[1:2,1:2])
}

# Priors for fixed effects regression coefficients
for (k in 1:17) {
  beta[k] ~ dflat()
}

# Priors for giver-receiver variance-covariance matrix
TAU_gr[1:2,1:2] ~ dwish(R_gr[1:2,1:2],2)
COV_gr[1:2,1:2] <- inverse(TAU_gr[,])
```

```
  # Priors for relationship variance-covariance matrix
  TAU_dd[1:2,1:2] <- inverse(COV_dd[1:2,1:2])
  COV_dd[1,1] <- sigma2_d
  COV_dd[1,2] <- sigma_dd
  COV_dd[2,1] <- sigma_dd
  COV_dd[2,2] <- sigma2_d
  sigma_dd <- rho_dd*sigma2_d
  sigma2_d <- 1/tau_d
  tau_d ~ dgamma(0.001,0.001)
  rho_dd ~ dunif(-1,1)

}
```

The file begins with the `model{}` statement and all subsequent statements are written within its braces. We shall explain these individual statements below. However, first it is important to realize that we arrange and model the data in a "dyadic setup" whereby there is one record per dyad and where the counts from household A to B and from household B to A are stored in two separate outcome variables. We shall therefore implement the SRM as bivariate response model. An alternative approach would be to arrange the model and data in a "unique relationship setup" where there is one record per directed relationship and all the counts are stored in a single outcome variable. In this case, the SRM would be implemented as a univariate response model. An analogy is the modeling of longitudinal panel data where one can model the data either in wide form (one record per individual and responses stored in separate outcome variables for each occasion) or long form (one record per individual-occasion and all responses stored in a single outcome variable) and where one therefore fits a multivariate or univariate response model, respectively.

We have indicated the different parts of the above model statement with WinBUGS comments. (WinBUGS comments begin with the # symbol.)

Dyadic response distributions

The dyad-level loop `for(d in 1:300){}` loops over the 300 dyads in the data. We specify four dyad-level statements within this loop.

First, we declare the number of gifts given from the first household in dyad `d` to the second `giftsAB[d]` to be Poisson distributed `dpois()` with mean `muAB[d]`.

Second, we repeat this statement for the number of gifts given in the other direction, from the second household in the dyad to the first.

Third, we specify the mean `muAB[j]` to be a log-linear function of the offset `offset[d]`, the intercept, the 16 covariates, and the giver, receiver and relationship random effects, `gr[hidB[d],1]`, `gr[hidA[d],2]` and `dd[d,2]`.[iii] The covariates appear in the model

in the same order in which they appear in Table 2. The covariate vectors beginning with `h` (`hgame[]`, `hfish[]` and so on) are 25×1 vectors with one element per household, while the covariate vectors beginning with `d` (`drel1[]`, `drel2[]` and so on) are 300×1 vectors with one element per dyad. The nested indexing `hidA[d]` and `hidB[d]` associated with the household vectors are used to "look up" and return the household identifier `h` associated with dyad `d`. The giver-receiver random effects matrix `gr[]` is a 25×2 matrix with one row per household and where the first column refers to the giver random effects and the second the receiver random effects. The relationship random effects matrix `dd[]` is a 300×2 matrix with one row per dyad and where the first column stores the relationship effects from the first to the second household in the dyad, while the second column stores the relationship effects from the second household to the first household in the dyad.

Fourth, we repeat the third statement for the number of gifts given in the other direction, from the second household in the dyad to the first.

Giver and receiver bivariate normal random effects

The household-level loop `for(h in 1:25){}` loops over the 25 households in the data. The giver and receiver random effects `gr[h,1:2]` are specified as bivariate normally distributed `dmnorm(,)` with zero mean vector `zero[1:2]` and 2×2 giver-receiver precision matrix `TAU_gr[1:2,1:2]`.[iv] (The precision matrix is simply the inverse of the variance-covariance matrix.) Immediately after the loop, we specify the vector `zero` to take fixed values of 0.

Relationship bivariate normal random effects

The dyad-level loop `for(d in 1:300){}` loops over the 300 dyads in the data. The relationship random effects `dd[d,1:2]` are specified as bivariate normally distributed `dmnorm(,)` with zero mean vector `zero[1:2]` and 2×2 relationship precision matrix `TAU_dd[1:2,1:2]`.

Priors for fixed effects regression coefficients

The parameter-level loop `for(k in 1:20){}` loops over the 20 regression coefficients in the model. We specify non-informative flat `dflat()` prior distributions for all coefficients.

Priors for giver-receiver variance-covariance matrix

We specify the giver-receiver precision matrix `TAU_gr[1:2,1:2]` to be Wishart `dwish()` distributed with scale matrix `R_gr[1:2,1:2]` and `2` degrees of freedom. We then define the giver-receiver covariance matrix `COV_gr[1:2,1:2]` to be the matrix inverse `inverse()` of this precision matrix.

Priors for relationship variance-covariance matrix

We define the relationship precision matrix `TAU_dd[1:2,1:2]` as the matrix inverse `inverse()` of the relationship covariance matrix `COV_dd[i,1:2,1:2]`. We specify the relationship variances, `COV_dd[1,1]` and `COV_dd[2,2]`, to be equal to the scalar `sigma2_d`. We specify the covariance matrix to be symmetric by setting the covariances `COV_dd[1,2]` and `COV_dd[2,1]` to be equal to the scalar `sigma_dd`. We then define this relationship covariance as equal to the relationship correlation `rho_dd` multiplied by the relationship variance `sigma2_d`. We define this relationship variance as the reciprocal of the relationship precision `tau_d`. We specify this precision to be gamma `dgamma()` distributed with diffuse shape parameters `0.001` and `0.001`. We specify the relationship correlation to be uniform `dunif()` distributed on the domain `−1` to `1`.

Data file

The "data file", named `data2.txt`, specifies the data as a series of arrays written within a single `list()` structure:

```
list(
   hidA=c(1,1,1,1,1,1,1,1,1,1,...),
   hidB=c(2,3,4,5,6,7,8,9,10,11,...),
   giftsAB=c(0,6,2,4,8,2,1,0,10,1,...),
   giftsBA=c(4,31,5,2,2,1,2,1,110,0,...),
   offset=c(0.000,-0.003,-0.019,0.000,-0.003,0.000,0.000,...),
   drel1=c(0,0,0,0,1,0,0,0,1,0,...),
   drel2=c(0,1,1,1,0,0,0,0,0,1,...),
   drel3=c(1,0,0,0,0,0,0,0,0,0,...),
   drel4=c(0,0,0,0,0,0,1,1,0,0,...),
   dlndist=c(-2.790,-2.817,-1.886,-1.892,-3.499,-1.853,...),
   dass=c(0.000,0.044,0.025,0.011,0.022,0.071,0.046,0.003,...),
   d0125=c(0,0,0,0,0,0,0,0,0,0,...)
   hgame=c(0.050,0.250,2.290,0.040,0.070,0.030,0.270,0.040,...),
   hfish=c(0.060,0.170,0.660,0.430,0.120,0.200,0.740,0.160,...),
   hpigs=c(0.000,1.750,5.750,1.500,1.250,2.500,3.000,2.000,...),
   hwealth=c(14.162,27.405,9.900,7.267,9.982,16.186,8.068,...),
   hpastor=c(0,0,0,0,0,0,0,0,0,0,...),
   R_gr=structure(.Data=c(1,0,0,1),.Dim=c(2,2)),
)
```

The file contains 17 variables each stored as a separate list `c()`. We display the first 10 elements (data values) of each list and have inserted `...` to denote the subsequent omitted elements. The variables `hidA` through `d0125` are dyad-level variables and are stored in lists of length 300. The variables `hgame` through `hpastor` are household level variables and are stored in lists of length 25. The final entry `R_gr` is the scale matrix associated with the Wishart prior for the giver-receiver covariance matrix.

Initial values file

The "initial values file", named `inits2.txt`, specifies the initial values for the model parameters as a series of scalars within a single `list()` structure:

```
list(
   beta=c(0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0),
   TAU_gr=structure(.Data=c(2,0,0,2),.Dim=c(2,2)),
   tau_d=1.333,rho_dd=0.500
)
```

We set the initial values for the 17 coefficients to 0. The initial values for the giver-receiver precision matrix `TAU_gr` correspond to specifying giver and receiver variances of 0.5 and a generalized reciprocity of 0. The initial value for the relationship precision `tau_d` of 1.333 corresponds to a relationship variance of 0.75. The initial value for the dyadic reciprocity `rho_dd` is 0.5. These are somewhat arbitrary choices and so we specify a long burn-in of 50,000 iterations to minimize the sensitivity of the monitoring iterations to the initial values. Nonetheless, it is good practice to test the sensitivity of the model results to different sets of initial values.

Script file

The "script file", named `script2.txt`, specifies a series of commands to load the model specification file, data file and initial values file described above and to then fit the model and display the model results:

```
display('log')
check('C:/data/model2.txt')
data('C:/data/data2.txt')
compile(1)
inits(1,'C:/data/inits2.txt')
gen.inits()
update(50000)
set('beta')
set('COV_gr')
```

```
set('COV_dd')
set('gr')
set('dd')
thin.samples(100)
dic.set()
update(100000)
dic.stats()
stats(*)
coda(*,'C:/data/out2)
save('C:/data/log2.txt')
quit()
```

The `display('log')` command opens a log file where the WinBUGS output will be saved. The `check()` command checks that the syntax in the model specification file is syntactically correct. The `data()` command loads the data file. The `compile(1)` command compiles a single chain while the `inits(1,)` command loads the initial values file for this chain. The `gen.inits()` command generates random initial values for any uninitialized chains, which in this example are the chains for the giver, receiver and relationship random effects.[v] The first `update()` command updates the chain with the burn-in iterations. We specify a burn-in of `50000` iterations so that the chains can converge to their stationary distributions.[vi] The `set()` commands specify the parameters to be monitored. In this example, we chose to monitor both the parameters and the random effects. The `thin.samples()` command retains only every `100`th iteration for inference. The `dic.set()` command calculates the DIC statistic. The second `update()` command updates the chain with the monitoring iterations. We specify a monitoring chain of `100000` iterations to ensure that the chains fully explore the posterior distributions.[vii] Upon completion, the `dic.stats()` command displays the DIC statistic while the `stats(*)` command displays posterior summaries for the monitored parameters including their means and standard deviations. The `coda(*,)` command writes the sampled values of the monitored parameters to two files: `out21.txt` and `out2Index.txt`. The first file includes the sampled values for the parameters, stacked sequentially. The second file saves the ordering of the saved parameters. The sampled values can be imported as data into any general-purpose statistical software package to produce plots of the model results or to perform additional calculations. The `save()` command saves the log file. The `quit()` command quits WinBUGS.

Model results

To fit the model, you must first save `model2.txt`, `data2.txt`, `inits2.txt` and `script2.txt` to `C:/data`. If you choose an alternative directory, you will need to edit the directory locations specified in `script2.txt`. Next, open WinBUGS, then open (`File > Open`) the `script2.txt` script file. You will need to select `Text(*.txt)` from the file type drop-down list located in the bottom right-hand corner of the File Open window. Fit the model by running the script file then fit the model by running the script file (`Model >`

Script).[viii] Upon completion, a table of posterior summary estimates of the parameters and giver, receiver and relationship random effects will be written to the log file `log.txt`. The Model 2 results presented in Table 2 of the paper are the results obtained from this log file. A partial listing of these results is presented below.[ix] The posterior mean, standard deviation 2.5th, 50th and 97.5th quantiles for each parameter are displayed.

node	mean	sd	2.50%	median	97.50%
beta[1]	-0.9212	0.634	-2.176	-0.8761	0.237
beta[2]	0.4496	0.08449	0.2737	0.4506	0.6148
beta[3]	0.2693	0.7691	-1.322	0.2512	1.807
beta[4]	0.1176	0.05357	0.01295	0.1194	0.2191
beta[5]	0.005223	0.0241	-0.03884	0.005489	0.05344
beta[6]	-0.09501	0.06716	-0.2225	-0.09633	0.04697
beta[7]	-0.7673	0.5756	-1.93	-0.7683	0.3465
beta[8]	-0.05593	0.04429	-0.1389	-0.05747	0.02971
beta[9]	-0.04774	0.01868	-0.08529	-0.04772	-0.01175
beta[10]	0.7851	0.3747	0.04726	0.7821	1.539
beta[11]	1.471	0.2559	0.9639	1.474	1.972
beta[12]	0.9441	0.1709	0.611	0.9425	1.298
beta[13]	0.2711	0.1423	0.004566	0.2672	0.5358
beta[14]	0.01005	0.1353	-0.2589	0.01271	0.2681
beta[15]	-0.6279	0.07978	-0.7844	-0.6273	-0.4582
beta[16]	4.016	0.6524	2.733	3.994	5.358
beta[17]	2.465	0.6242	1.244	2.464	3.69
COV_gr[1,1]	0.3041	0.1168	0.1461	0.2815	0.5861
COV_gr[1,2]	0.01919	0.06565	-0.1101	0.01633	0.1668
COV_gr[2,1]	0.01919	0.06565	-0.1101	0.01633	0.1668
COV_gr[2,2]	0.1773	0.07221	0.08341	0.1647	0.3568
COV_dd[1,1]	0.2947	0.04386	0.2165	0.2933	0.385
COV_dd[1,2]	0.2275	0.04626	0.1451	0.2268	0.3236
COV_dd[2,1]	0.2275	0.04626	0.1451	0.2268	0.3236
COV_dd[2,2]	0.2947	0.04386	0.2165	0.2933	0.385
gr[1,1]	0.006127	0.2799	-0.5885	0.01231	0.573
gr[1,2]	-0.4557	0.2224	-0.8996	-0.4622	-0.007019
gr[2,1]	0.3819	0.3537	-0.2981	0.3803	1.068
gr[2,2]	0.09682	0.2786	-0.4375	0.09459	0.6409
...					
gr[25,1]	0.1232	0.291	-0.4357	0.1329	0.6945
gr[25,2]	0.2711	0.2222	-0.1657	0.2594	0.7519
dd[1,1]	0.03277	0.4441	-0.8713	0.04425	0.8478
dd[1,2]	0.1612	0.4096	-0.6426	0.1508	0.9772
dd[2,1]	0.9027	0.3477	0.2557	0.8994	1.615
dd[2,2]	0.8281	0.2602	0.3345	0.8328	1.329
...					
dd[300,1]	0.1197	0.4632	-0.7817	0.115	1.033
dd[300,2]	0.04203	0.4693	-0.8991	0.03652	0.9767

References

Lunn, D., Jackson, C., Best, N., Thomas, A., Spiegelhalter, D., 2012. The BUGS Book: A Practical Introduction to Bayesian Analysis. Chapman & Hall/CRC Texts in Statistical Science.

Ntzoufras, I., 2009. Bayesian Modeling Using WinBUGS. John Wiley & Sons, New York.

Spiegelhalter, D.J., Thomas, A., Best, N.G., Lunn, D. (2003). WinBUGS Version 1.4 User Manual. MRC Biostatistics Unit, Cambridge. URL http://www.mrc-bsu.cam.ac.uk/bugs/.

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[i] WinBUGS can also be used interactively via its graphical user interface (GUI). However, we prefer to fit models in batch model via script files as this facilitates replicating analyses at a later date.

[ii] While our preference is to call WinBUGS from within Stata using the user written winbugs command (Thompson et al., 2006), in this file we demonstrate how to use WinBUGS as a standalone package.

[iii] The assignment sign <− corresponds to the = sign used in the algebraic representation of the model.

[iv] A quirk of WinBUGS is that normal distributions are parameterized in terms of means and precisions rather than means and variances.

[v] In Bayesian estimation, the random effects are viewed in the same way as parameters, as unknown random variables.

[vi] We judged convergence by informal visual assessments of the parameter chains (not shown here) and through examining standard MCMC convergence diagnostics. A burn-in chain of 50,000 was found to be sufficient for all models.

[vii] As with convergence, we judged whether the parameter chains were mixing sufficiently through informal visual assessments of the parameter chains and through examining MCMC diagnostics. A monitoring chain of 100,000 was found to be sufficient for all models.

[viii] The model took approximately two hours to run on a 2.66Ghz Intel Xeon X7460 processer running on Windows Server 2008.

[ix] We have removed three columns (MC error, start and sample) from the table so that the output fits on the page.